

# Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano

Vol. 132 (1991), n. 24, pag. 309-335

Milano, ottobre 1992

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## Palaeoenvironment of extraordinary fossil biotas from the Upper Triassic of Italy

BRW 282586

**Abstract** — During the last 20 years, many exceptional fossiliferous levels have been discovered in the Upper Triassic of Lombardy, Northern Italy. The assemblages mainly comprise superbly preserved arthropods, vertebrate skeletons in anatomical connection, and also rare soft bodied organisms. Invertebrates are represented by worms, molluscs, crustaceans, insects and echinoderms, whereas vertebrates include fishes and reptiles. The associations are comprised of both continental and marine organisms, and reveal many previously unknown taxa. This paper is an attempt to produce a palaeoenvironmental interpretation of these faunae, through the integration of sedimentological and palaeontological data.

The fossiliferous associations are preserved both within calcareous black shales (part of the Calcare di Zorzino) and in younger laminated claystones (Lower Argillite di Riva di Solto, «Rhaetic Facies»).

The older fossiliferous associations were preserved during a carbonate depositional phase characterized by emerging areas, large stromatolitic tidal flats, shallow platform lagoons and marginal reefs. The reefs were dominated by algae, serpulid worms and other encrusting organisms and flanked by narrow, poorly oxygenated intraplatform depressions. The fossiliferous beds deposited within these depressions contain mainly nectonic crustaceans and bony fishes. The majority of these faunae adapted to reef environment, but lagoon and terrestrial organisms are also included. Vertebrate associations show some of the most ancient known flying reptiles. The ecological composition of the continental vertebrate faunas was probably similar to that of modern tropical keys.

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The carbonate deposition was terminated by an important transgression, which drowned many carbonate highs, killed the wave resistant reefs and produced a larger argillaceous basin. This phase was probably characterized by nutrient rich sea waters with reduced salinity. The coeval fossiliferous levels record the disappearance of the reef adapted faunae, and the diffusion of organisms adapted to poorly oxygenated, nutrient rich, soft sea bottoms. Particularly important changes are demonstrated by the crustacean associations, which were now dominated by benthic forms.

**Riassunto** — Durante l'ultimo ventennio, le successioni bacinali del Triassico superiore affioranti nelle Prealpi Lombarde hanno rivelato una imprevista ricchezza paleontologica. In molte località delle provincie di Bergamo e Brescia sono stati infatti scoperti importanti giacimenti paleontologici, che hanno fornito ricche associazioni di organismi che raramente si incontrano allo stato fossile, quali invertebrati con esoscheletro chitinoso, scheletri di vertebrati in connessione anatomica e rari organismi a corpo molle. Le faune rinvenute comprendono forme sia continentali che marine; gli invertebrati sono rappresentati da vermi, molluschi, crostacei, insetti ed echinodermi, mentre i vertebrati comprendono pesci cartilaginei, pesci ossei e rettili.

Questo lavoro integra i numerosi ma dispersi dati bibliografici con dati geologici e paleontologici originali, al fine di ricostruire il contesto paleoambientale di queste straordinarie faune.

La sintesi fra lo studio paleoecologico delle faune fossilizzate nelle successioni bacinali e l'analisi delle coeve unità di piattaforma e di margine ha permesso infatti una plausibile ricostruzione paleoambientale. I giacimenti paleontologici sono stati scoperti sia all'interno di unità bacinali carbonatiche (Calcere di Zorzino), sia in successioni argillose più recenti (Argillite di Riva di Solto). Queste diverse formazioni riflettono importanti variazioni paleoambientali e contengono associazioni faunistiche alquanto diverse. Dal punto di vista della stratigrafia sequenziale questi cambiamenti corrispondono probabilmente alla transizione fra un periodo di stazionamento basso del livello marino relativo ed una fase trasgressiva.

La fase totalmente carbonatica di stazionamento basso era caratterizzata da un clima caldo e arido. In questa fase si svilupparono estese pianure di marea che passavano lateralmente a lagune carbonatiche e a scogliere resistenti al moto ondoso. Queste scogliere erano dominate da alghe, vermi tubiformi (serpulidi), foraminiferi ed altri organismi incrostanti, con una ridotta presenza di coralli. Le scogliere fiancheggiavano piccoli bacini, profondi alcune centinaia di metri, in cui si ridepositavano ingenti quantità di carbonati provenienti dalle contigue piattaforme. Questi bacini erano caratterizzati da una scarsa ossigenazione al fondo e talora da condizioni anossiche, che hanno permesso la preservazione delle straordinarie associazioni faunistiche dominate da crostacei decapodi neotonici e pesci ossei. Fra i rettili spiccano alcune delle più antiche forme volanti conosciute. Buona parte delle forme preservate nelle successioni bacinali erano probabilmente adattate ai biotopi di scogliera, ricchi di anfratti e con una complessa catena trofica. Altri organismi vivevano nelle lagune di piattaforma o su aree emerse, probabilmente simili agli attuali isolotti tropicali. La deposizione carbonatica fu interrotta nel Norico superiore da un'ampia trasgressione. Gli alti carbonatici e le scogliere ad incrostanti annegarono, e si formò un più vasto bacino argilloso. Numerosi dati geochimici suggeriscono che questa fase fu probabilmente caratterizzata da acque marine ricche di nutrienti e con ridotta salinità. Anche le associazioni faunistiche preservate nei bacini testimoniano importanti cambiamenti: scomparvero infatti gli organismi terrestri e subirono una drastica riduzione quelli adattati all'ambiente di scogliera; le associazioni ittologiche presentano inoltre una ridotta diversità tassonomica; i crostacei decapodi evidenziano invece un turn-over di taxa ed una maggiore differenziazione rispetto alle associazioni precedenti, con una netta prevalenza delle forme bentoniche.

**Key words:** Lagerstätten, Stratigraphy, Norian, Rhactian, Sedimentology, Northern Italy, Alps.

## Introduction

Exceptional depositional conditions allowing the preservation of soft bodied and poorly mineralized invertebrates and articulated vertebrate skeletons have been quite rare in the geological history. Such lucky conditions at time developed, preserving palaeontological associations rarely found in the fossil record («conservative lagerstätten», Seilacher et al., 1985). Despite their rareness, these levels harbour an important portion of the palaeontological record, and their lack would dramatically reduce our knowledge of life history. This contribution synthetically deals with some of these lagerstätten, discovered in the Upper Triassic (Norian) of Lombardy, Northern Italy. Both continental and marine organisms are found in these Italian lagerstätten, including many previously unknown taxa. Invertebrates are represented by worms, crustaceans, insects, echinoderms and molluscs, whereas vertebrate include fishes and reptiles. These faunae bring new light on the evolutionary history of some poorly known taxa, whereas integration of palaeoecological and sedimentological analysis can produce accurate environmental reconstruction.

These allocthonous associations were preserved in poorly oxygenated depressions, associated with carbonate platforms. The environmental conditions that enabled the exceptional fossilizations also made these levels important source rocks for hydrocarbons (Mattavelli & Novelli, 1987; Burchell & Stefani 1992; Stefani & Burchell, 1990). These fossiliferous levels have been the subject of a number of publications by both palaeontologists and geologists of several universities and museums (in alphabetical order: Universities of Berkeley, Bologna, Ferrara, Milan, Oxford, Pavia, and Perugia; Museums of Bergamo, Brescia, London, Milan and Stuttgart). Excavations were mainly carried on by teams of the Milan University; lesser excavations were carried on by the Bergamo and Milan Museums. Palaeontological materials are presently stored in the Bergamo, Brescia and Milan Museums and in local Museums.

This paper is an attempt to produce a palaeoenvironmental interpretation of these faunae through the integration of published analytical informations with original analysis. However, researches are still in progress, and a certain amount of palaeontological material still remains to be described; this paper is therefore intended to provide only a general preliminary picture of the environmental framework of these outstanding faunae.

## Stratigraphy and depositional evolution

### Palaeogeographic Framework

The Norian fossiliferous levels outcrop in the Western part of the Southern Alps (Fig. 1). During the Triassic this area was part of the future African continental margin. In the Norian, the Italian region and the adjacent areas were characterized by broad carbonate platforms and islands, interspaced with a few deeper water, open marine basins (Bosellini & Hsu, 1973) (e.g. Halstatt, Budva-Pindo and Lagonegro). These deep water troughs were probably connected to the east with the oceanic areas of the closing Palaeotethys (Fig. 2). Other localized depressions developed in intraplat-

form settings (Austro- and Southern-Alpine areas), where exceptional fossilizations sometime occurred. The carbonate platforms areas laterally graded into evaporative settings and eventually passed to the European epicontinental basins, where mixed terrigenous-evaporitic Keuper successions accumulated (Ziegler, 1982). These depositional settings were developed in a tropical belt, characterized by a warm and arid climate.

During the Upper Norian times, a widespread transgression occurred; large platform sectors experienced a partial drowning, evaporitic deposition ceased on wide areas, whilst substantial argillaceous sedimentation started (the so called «Rhaetic Facies»). In several Austro and Southern Alpine areas, the intraplatform carbonate depressions coalesced to form larger argillaceous basins. Other carbonate platform areas however survived, often experiencing some deepening. In the meantime carbonate platforms were born on former evaporitic or continental areas (Fazzuoli & Stefani, 1991). The argillaceous basins, while receiving important terrigenous influx, remained comparatively isolated from open marine settings, because the interposition of large carbonate platforms. These Upper Norian environmental changes were probably matched with an evolution toward moister conditions (Stefani & Burchell, 1990). This transgression was followed by a renewed shallowing evolution. The end of the Triassic therefore saw the development of a new generation of widespread carbonate platforms, whilst terrigenous sedimentation ceased.

The fossiliferous levels were deposited both during the wholly carbonate depositional stage and during the initial transgressive phase of argillaceous sedimentation. The different ecological conditions are reflected by significant changes in the palaeontological associations. The sequence stratigraphic interpretation (Sarg, 1988) of these successions (Stefani, 1989) suggests that this environmental change reflect the transition between low-stand and transgressive phases, within the same depositional sequence. The environmental conditions prone to the exceptional fossilizations eventually vanished during the uppermost Triassic shallowing, and therefore no lagerstätten are known near the Triassic-Jurassic boundary.

### **The Carbonate Depositional Phase**

During the Norian, the Southern Alpine region was part of a broad carbonate platform. Subsidence rates, even if highly variable in both time and space, were generally elevated, allowing the accumulation of thick (between 200 and 2000 m) successions of shallow water dolomites (Dolomia Principale). In highly subsiding regions (Lombardy, Friuli), sedimentation rates were however often unable to keep pace with strong relative sea level rise; deeper depressions therefore progressively developed, largely controlled by palaeotectonic movements (Jadoul & Rossi, 1982; Jadoul, 1986), possibly transtensive in nature.

In these depressions thick (up to more than one km) basinal sediments accumulated (e.g. Gruppo dell'Aralalta, Jadoul 1986, see Fig. 3, 4), characterized by monotonous micritic successions (Calcare di Zorzino, Casati, 1964) and, in marginal settings, by huge volumes of resedimented breccias.

The depressions were interspaced with shallow water carbonate highs, flanked by buildup margins or by steep fault-escarpments. The interplay between relative sea level rise and sediment accumulation produced a complex evolution. Whereas progradation of margin and slope environments eventually closed some minor depressions, the majority of the basins experienced a deepening and widening evolution. In the Lombardy region, at the end of the wholly carbonate depositional phase, the extension of basinal areas probably exceeded that of the carbonate highs. Basinal successions therefore generally progressively overlaid carbonate platform deposits. However, basinal units may locally represent the lateral time-equivalent of the whole of the Norian shallow water carbonates (e.g. some basinal successions — «Facies eteropiche», Boni & Cassinis, 1973 — outcropping in the north-eastern Brescia Province — Rossetti, 1966; Burchell & Stefani, 1992). The exceptional faunal assemblages were preserved in the intraplatform depression bottoms, during periods of strong sea-water stratification and anoxia. These anoxic phases were particularly common during the last phase of wholly carbonate sedimentation. Therefore the fossiliferous beds, even if present at lower levels within the basinal successions, are particularly abundant near the top of the carbonate units. True anoxic episodes were otherwise comparatively uncommon. The great majority of the basinal carbonate successions therefore show a very poor palaeontological content. The average fossiliferous content is actually so reduced that no faunas at all were known in these succession up to the sixties.

### **The Terrigenous - Carbonate Depositional Phase**

In the majority of the Lombardy region, during the Upper Norian, calcareous deposition was interrupted by generalized transgression; carbonate highs were drowned, and carbonate production was interrupted; the former depressions therefore coalesced to form a larger argillaceous basin (Lombardy Basin). Transgression was matched with the starting of substantial argillaceous sedimentation (base of Lower Member of the Argillite di Riva di Solto, Stefani, 1989). Shallow water carbonate sedimentation generally survived in the regions to the west (Varese Province, Gnaccolini, 1965) and to the east (Trento Platform, Bosellini et al., 1985) of the Lombardy Basin. These carbonate platform regions often show some deepening and a reduced importance of the early diagenetic dolomitization (Iannace & Frisia, 1991; Stefani & Burchell, 1991). During the transgressive phase, condensed levels were deposited on the palaeo-highs, whilst thick argillaceous successions accumulated in the adjacent depressions. In the transgression and basal highstand phases the basin was often characterized by poorly oxygenated to anoxic conditions. Important faunal association were therefore again preserved. The Lombardy Basin subsequently accumulated up to two km of mixed carbonate-argillaceous sediments (Argillite di Riva di Solto, Calcare di Zu, Gnaccolini, 1965; Calcare di Tremalzo, Stefani & Golfieri, 1989). The basin experienced a shallowing evolution (Lakew, 1990; Stefani, 1989) and eventually returned to shallow water carbonate sedimentation during the later Rhaetic (Casati & Gaetani, 1979).

These successions are generally characterized by asymmetric marl-limestones cycles (Masetti et al., 1989). Regular sedimentary cyclicity is recorded in all the studied depositional phases. This cyclicity reflects important environmental fluctuations and was certainly influenced by the eustatic oscillations recorded in the platform successions (Bosellini et al., 1985; Burchell et al., 1990). Tectonic and autocyclic mechanisms also played a role in controlling the depositional dynamics. The high frequency environmental fluctuations certainly affected the biota composition, but detailed discussion on sedimentary cyclicity exceeds the purposes of this article.

### **The faunae and their palaeoenvironment**

The following paragraphs are aimed to reconstruct the palaeoenvironmental framework of the study faunal associations through integration of sedimentological and palaeontological analysis. Detailed palaeogeographic reconstruction of the study region is however difficult because of the lack of reliable time markers and because of the importance of the tectonic shortening (Castellarin & Picotti, 1990).

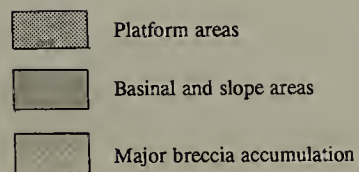
The study fossiliferous levels reveal plenty of information on the ecological features of the surrounding biotopes. Some caution in the interpretation is however needed. The allocthonous nature of the thanatocenosis makes the synecological argumentation difficult. The faunae fossilized during uncommon events of basinal anoxia; the faunal associations therefore probably reflect unusual ecological conditions; for instance, stronger seawater stratification probably reduced nutrient concentration in shallow water environments by damping the ecological recycling. Large amount of palaeontological material still wait to be excavated and described, and the fact that from time to time new taxa are discovered demonstrates that our palaeontological data set is still largely incomplete. Nevertheless the general palaeoenvironmental framework is quite clear.

## **The Wholly Carbonate Environments and Their Biota (Dolomia Principale and Calcare di Zorzino)**

### **The Environmental Framework**

During the Norian carbonate sedimentation phase, the Southern Alps were characterized by a complex array of sedimentary environments. Inner-platform zones are largely recorded in the central portion of the Southern Alps (Dolomia Principale of the Veneto Region). These wide, flat areas were characterized by emerging islands and by large tidal flats, covered by stromatolitic cyanobacterial mats, sometimes still preserving dinosaur footprints (Mietto, 1985). The internal portion of the tidal flat was reached by sea-water only during severe storms, testified by muddy storm layers, and was the site of intense vadose diagenesis. Low-energy lagoons developed on other platform areas, probably under hypersaline conditions, with intense bioturbation and poorly diversified faunae dominated by large pelecypods (megalogontids) and gastropods (vortenias).

Fig. 1 — Present day distribution of the basinal and platform sediments deposited during the last phase of the Norian carbonate accumulation («palaeogeography» fossilized under the transgressive surface). Question marks indicate areas lacking outcrops or probably slightly older successions. The study area suffered an important tectonic shortening, and therefore present day distribution of the depositional units is quite different from the original palaeogeographic framework. Platform-basin transitions were expecially reactivated by the alpine compressional tectonics. The map is based on published works (Boni & Cassinis, 1973; Casati & Gaetani, 1979; Castellarin, 1981; Jadoul, 1990; Castellarin & Picotti, 1990) integrated with original unpublished geological mapping.



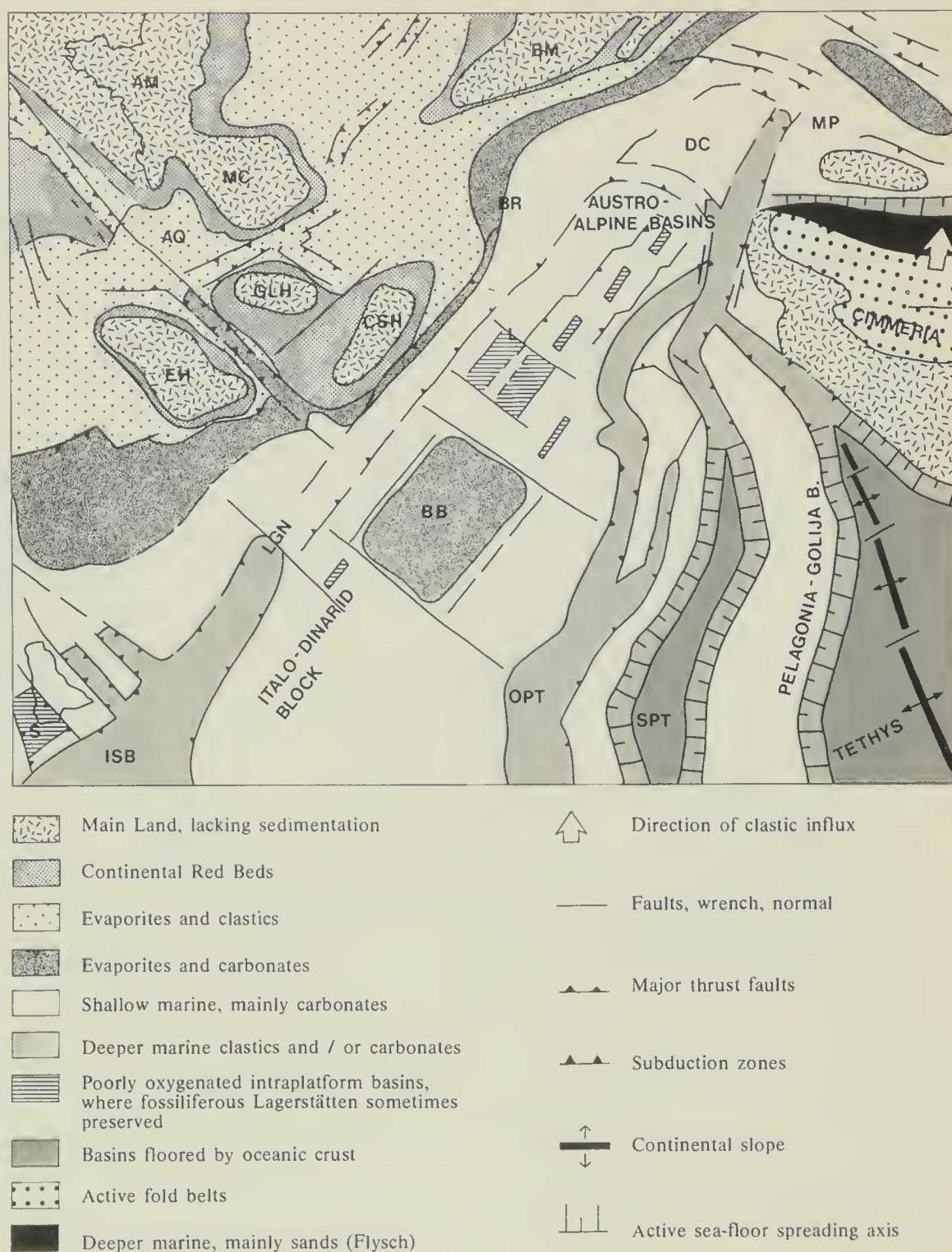


Fig. 2 — Synthetic palinspastic-palaeogeographic map of the Italian area and of the surrounding regions in Norian times, modified from Ziegler, 1988. The accuracy of the palaeogeographic reconstruction decreases moving from NW to SE. The study basins were part of a complex system of intraplateau depressions developed at the western termination of the Palaeotethys. AM) Armorican massif; AQ) Aquitaine basin; BB) Burano evaporitic basin; BM) Bohemian massif; BR) Briançonnais; CSH) Corsica - Sardinia high; DC) Dacides block; EH) Ebro high; GLH) Golf de Lion high; ISB) Ionian sea basin; L) Lombardy; LGN) Lagonegro trough; MC) Massive central; MP) Moesian platform; OPT) Olenos - Pindos trough; S) Streppanosa basin; SPT) Sub - Pelagonian trough.

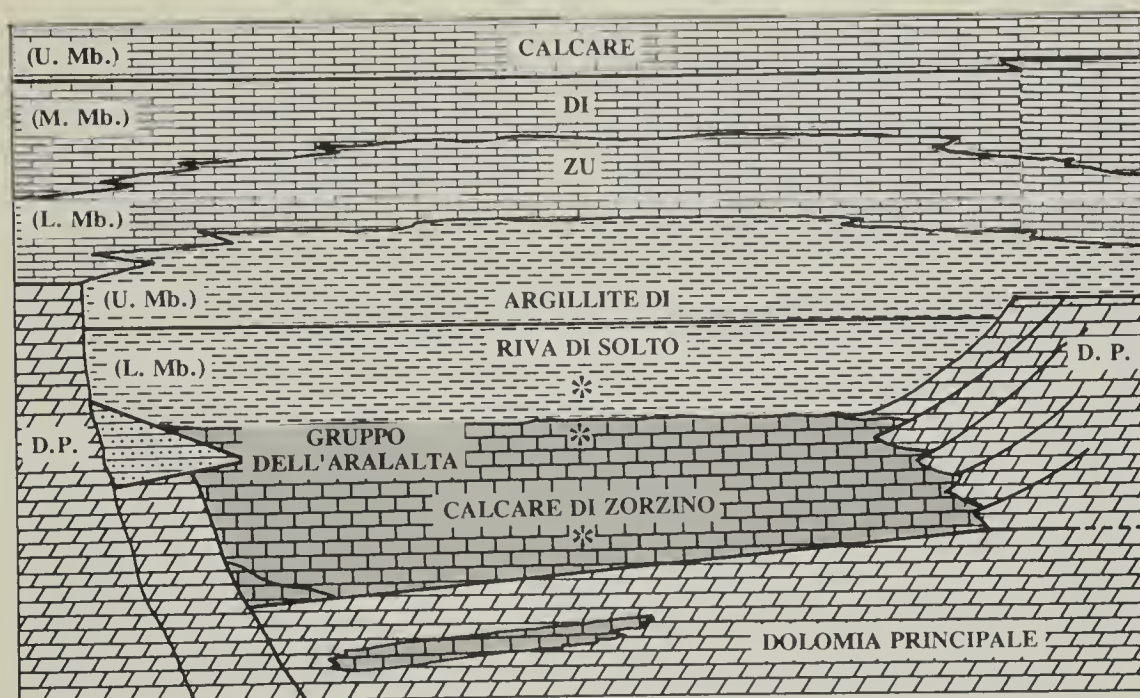


Fig. 3 – Lithostratigraphic scheme of the Norian-Rhaetian succession in Lombardy. Note the lateral transition between Norian carbonate platforms (Dolomia Principale) and the coeval basinal successions. \* = Fossiliferous levels.

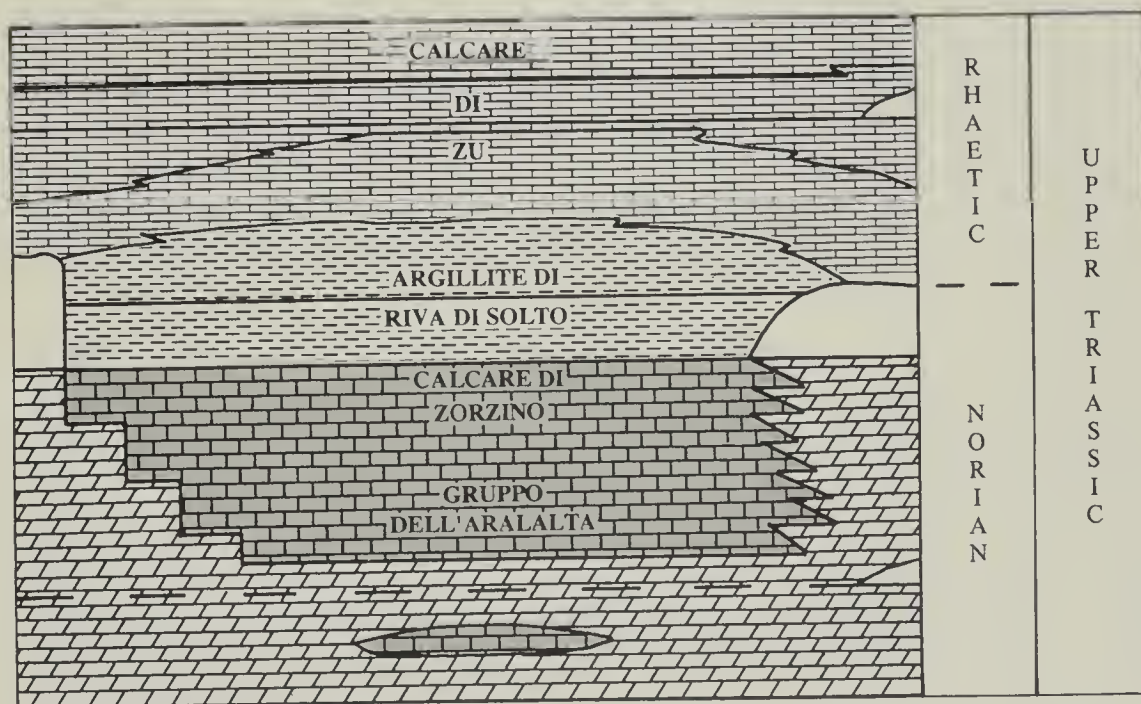


Fig. 4 – Chronostratigraphic interpretation of the Norian-Rhaetian succession. The two horizontal lines crossing the scheme correspond to two probable depositional sequence boundaries (Stefani, 1987). White spaces indicate non-depositional hiatus. There is no general agreement on the Norian-Rhaetian boundary. Here the base of the Rhaetian is located at the appearance of *Triasina hantkeni*. Note the megabreccia bodies, produced by «catastrophic» events, that controlled the back stepping evolution of some platform margin.

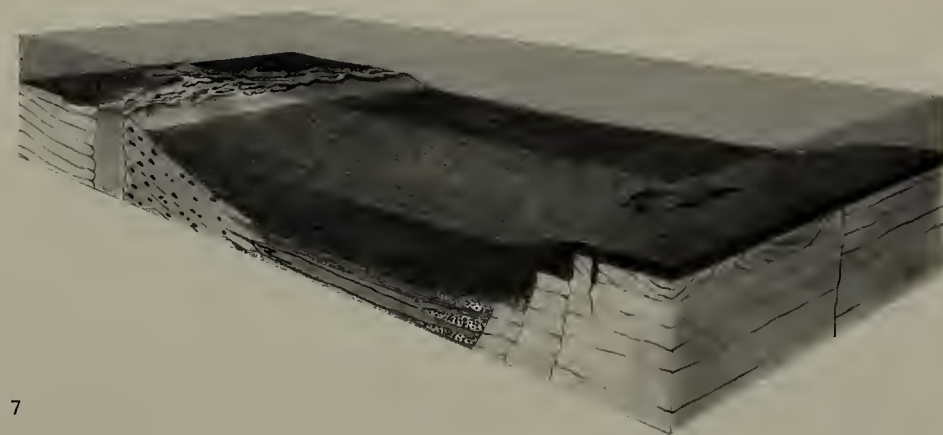
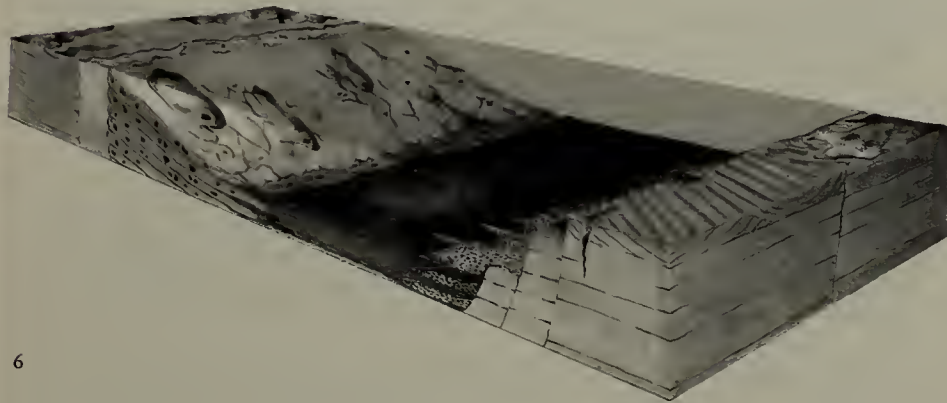
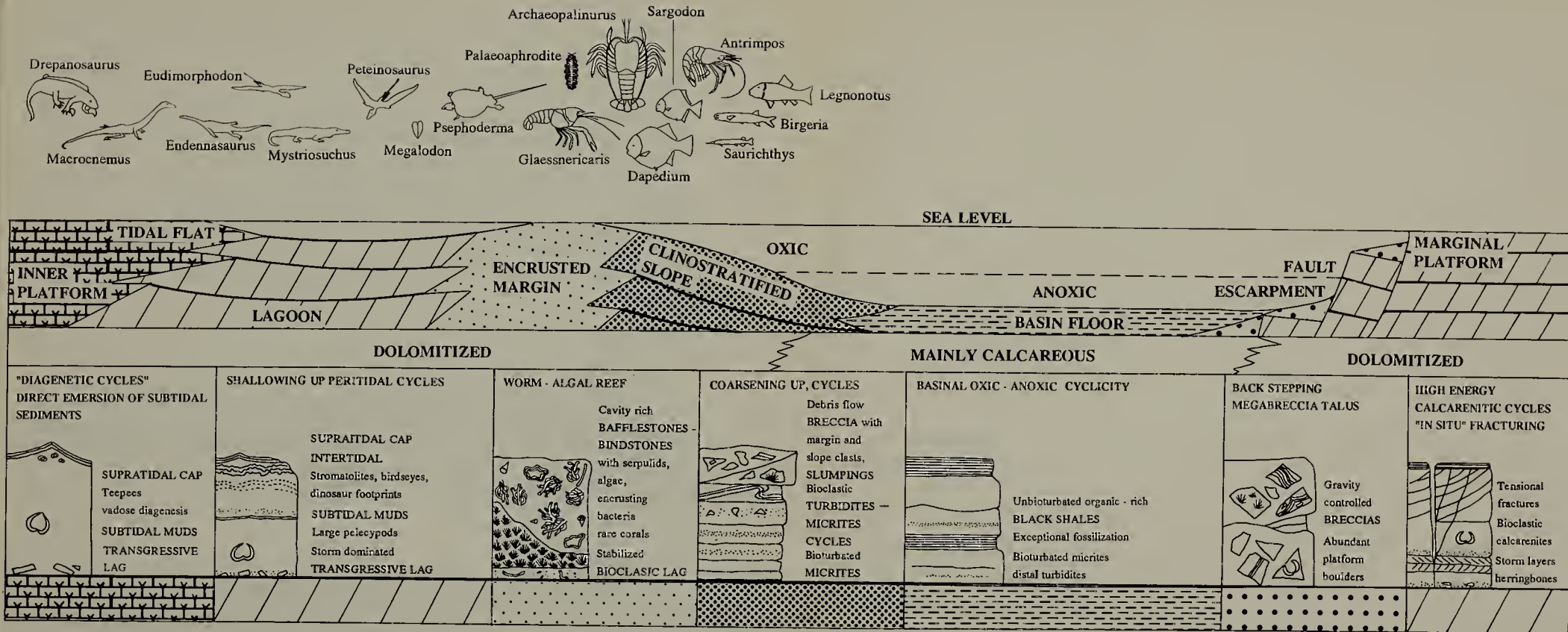
Tidal currents were generally not important, and low energy conditions largely dominated; storm events were however often recorded in the lagoonal successions. These widespread shallow water areas passed westwards into a complex patchwork of small basins (Lualdi & Tannoia, 1985; Jadoul, 1986), some kilometres to a few tens of kilometres wide, interspaced with small carbonate highs (Stefani & Burchell, 1990). These isolated highs were characterized by stromatolitic tidal flats and lagoons which were smaller but similar to those developed on wider platform areas; bioclastic shoals, rich in algae remains, were locally common. Platform-margin buildups (Cirilli & Tannoia, 1985; Jadoul, 1986, 1990) were generally formed by bindstones encrusted with «blue algae» and problematicas, and by boundstones made by huge amounts of tube-worms (serpulids). Subtidal columnar stromatolites were locally common. Other marginal buildups were dominated by bafflestones, with tube-like porostromata, tube-worms, and green algae (dasycladaceans). These bafflestones were associated with calcareous sponges and isolated corals. A large portion of the faunae preserved in the adjacent depressions probably adapted to these cavity-rich marginal environments (examples of marginal buildups are for instance well exposed by the western shore of the Como Lake, Cirilli & Tannoia, 1985). From an ecological point of view, these margins were quite different from the coeval coral rich reefs flanking open-marine basins (i.e. Dachstein Reefs, Zankl, 1971). These bio-encrusted margins were flanked by steep slopes, rapidly reaching considerable depths. Lateral migration of these slope locally produced spectacular clinostratified deposits (e.g. Valvestino outcrops, Picotti & Pini, 1988) similar to those known in the Triassic of the Dolomites (Bosellini, 1984; Bosellini & Stefani, 1992). Other platform areas were flanked by even steeper, abrupt fault escarpments, associated with huge volume of megabreccias (Giannotti, 1984; Jadoul, 1986; Jadoul & De Bonis, 1981), which often derived from the dismantling of older carbonates. The development of these marginal buildups was often remarkably different on the various sides of the same asymmetric basin (Fig. 5). The slope settings were often colonized by a variety of encrusting organisms, with algae associations giving up to worms and bacterial moving downslope into disphotic and aphotic zones. These margins flanked narrow depressions, several hundred metres deep and several kilometres wide, as testified by locally preserved depositional geometry. In near margin- settings resedimentation was important, with development of a continuous spectrum of depositional mechanisms, ranging from pure gravitational fall to turbiditic and debris flow processes (Lualdi & Tannoia, 1985; Jadoul 1986). Gravitational instability is also often testified by widespread slumping. The depression centres received only calcareous muds, exported from adjoining platforms as aragonithic oozes, as testified by the average elevated concentration of strontium (Calcare di Zorzino). These basins were characterized by strong water stratification, and by reduced wave motion, limited by the narrow wind-fetch.

Hypersaline conditions were often common, as testified by the occurrence of pseudomorphs of evaporitic mineral and by traces of sulphates (Stefani & Burchell, 1991; Jadoul oral communication). Basinal water was probably characterized by nutrient excess (Burchell 1988; Stefani & Burchell, 1990).

Fig. 5 — Perspective sketch of an idealized Norian carbonate basin. Note the symmetric nature of platform margins, largely controlled by palaeotectonic movements. Carbonate production was active on platforms, while anoxic conditions often developed in the basinal depressions.

Fig. 6 — Sketch of the relationships between the sedimentary environments and the faunae associations in an idealized Norian carbonate basin. The upper portion schematically illustrates some of the main components of the fauna, whereas the lower part depicts the different facies association typifying the various sedimentary environments (diagenetic cycles, peritidal lagoon cycles, bioencrusted reef deposits, base of the slope thickening up cycles, basinal oxic-anoxic cyclicity, megabreccias bodies associated to fault escarpments, high energy marginal platform settings).

Fig. 7 — Sketch of an idealized «Rhaetic» argillaceous basin. The lower argillaceous deposits overlapped the older carbonate slope, drowned by transgression (drowning unconformity associated with the transgressive surface). While in the depressions copious volumes of argillaceous clastics accumulated, on the drowned paleohighs condensed surfaces developed.



These Southern Alpine basinal depressions were isolated from oceanic zones, therefore open marine organisms, like ammonoids, «planktonic» pelecypods or radiolarians are extremely rare. The depressions aphotic bottoms were characterized by poorly oxygenated conditions, and therefore very poor autochthonous faunae were present, often testified only by bioturbation structures. The oxic-anoxic boundary was often very near the seabottom, and therefore deep bioturbation was uncommon. Oxic-anoxic cyclicity is often witnessed by regular alternation of bioturbated and unbioturbated levels. When anoxic conditions developed, oxic metabolism was interrupted, and even these organisms disappeared. Only reducing anoxic bacteria probably colonized these severe environments. In these conditions, biological recycling of organic matter was extremely reduced, allowing the exceptional fossilizations and the accumulation of important amount of organic matter.

### The Faunae

The faunae preserved in discrete horizons within the micritic basinal successions (Calcare di Zorzino) are dominated by crustaceans and fishes. Faunae are very rich in individual, but they often show a comparatively reduced taxonomic diversity. The main fossil localities are known in central-eastern Lombardy (Bergamo and Brescia provinces, e.g. Brembilla, Endenna, Cene and Magasa, cfr. Tintori et al., 1985).

### Invertebrates

Invertebrate faunae are dominated by crustaceans associations, particularly rich in decapods (Pinna, 1974, 1976; Garassino & Teruzzi, 1992). The decapod associations are generally dominated by nectonic forms. Swimming shrimp-like forms (e.g. *Antrimpos*, *Palaeodusa*) are often very abundant, whereas reptant forms, like small lobsters (*Archaeopalinurus*), are only locally common. Isopods crustaceans are rare, whereas epibenthic, semi-sessile scavenger thylacocephalan crustaceans (*Atropicaris*, *Microcaris*, *Clausocaris*, Arduini, 1988, 1992) are often comparatively abundant. Ophiuroids are locally common, whereas mollusca (pelecypods, gastropods) errant polychaete annelids (the sea-mice *Palaeoaphrodite*) and echinoids are rarer. «Planktonic» pelecypods and ammonoids are lacking.

### Vertebrates

Vertebrate skeletons are usually articulated. Bony fishes (Tintori et al., 1985) are mainly represented by small pholidophorids, together with margin adapted durophagous forms (pseudonodonts such as *Brembodus*, *Gibbodon*, *Eomesodon*, and semionotids like *Sargodon*, *Dandya*, *Dapedium*, *Paralepidotus* and *Semionotus*), coelacanth (*Holophagus*) and large predators (*Birgeria* and *Saurichthys*).

Cartilaginous fishes are represented by a small predator shark (*Pseudodolatias*), whose remains consist of articulated teeth rows (Tintori, 1980).

Reptiles are rarer but extremely interesting. Marine forms are represented by the large predator, alligator-like phytosaur *Mystriosuchus*, or by the turtle-like durophagous placodont *Psephoderma* (Pinna, 1979; Pinna & Nossotti, 1989). Terrestrial reptiles are represented by lizard-like archosauromorphs (the insectivorous *Macrocnemus*) and the tail-hooked diapsid *Drepanosaurus* (Pinna, 1980, 1984, 1986), the thecodont *Aetosaurus* (Wild, 1989) the arboreal eolacertilian *Vallesaurus* (Wild, 1989) and by the terrestrial or semiaquatic diapsid *Endennasaurus* (Renesto, 1984). The reptile association also shows the most ancient known flying reptiles (Wild, 1984), already ecologically specialized with insectivorous (*Eudimorphodon*) and fish-eater (*Peteinosaurus*) forms. Vertebrate coprolites are also represented in these associations.

### Palaeoecological Interpretation

The taxa preserved in these fossil associations can be ascribed to several palaeobiotopes, i.e. to the superficial basinal waters, to the platform margin environments, to the back-reef lagoons and finally to the emerging carbonate islands (fig. 6). Many uncertainties on the precise ecological characterization of individual taxa still remain, but the general framework is clear.

The organisms adapted to the superficial basinal waters, above the strong pycno- and thermo-cline, are probably represented by predators like as *Birgeria* and *Saurichthys*, and possibly by the shrimp *Antrimpos*. The majority of the organisms found within the basinal sediments however adapted to the cavity-rich reefs, both for shelter and/or for feeding. In these complex biotopes, rich in diversified ecological niches, probably lived the pholidophorid and durophagous fishes, benthic crustaceans, echinoids and errant polychaete annelids.

In the allocthonous basinal associations are also represented several non sessile organisms that probably lived mainly within the back reef lagoons, like as phytosaur and placodont reptiles.

The endobenthic organisms also lived in the back-reef lagoon environments; molluscs, as the megalodontids, were not generally transported into the intraplatform depression, and therefore they are not observed in the basinal units.

No large terrestrial vertebrate has been discovered, which probably reflect the comparatively isolated nature of these small islands and keys. These isolated subaereal biotopes were more easily reached by flying vertebrates (e.g. pterosaurs) or by semiaquatic (e.g. *Endennasaurus*) and small terrestrial (*Macrocnemus*, *Drepanosaurus*, *Aetosaurus*, *Vallesaurus*) forms than by larger continental organisms. The reduced extension of the island biotopes moreover reduced the availability of food for the predators at the height of the food chain. The ecological structure of reptile terrestrial coenosis, which includes small insectivorous or fish-eater forms, probably reflected an environment with reduced food availability. Alligator-like phytosaurs generally adapted to continental environment, but in the study environments they probably lived as lagoon-dweller predators. The general environmental framework was therefore probably quite similar to that of modern tropical keys. However is again worthy to remember the incompleteness of the palaeontological data.

## The Deepened Environments and Their Biota (Argillite di Riva di Solto)

### The Environmental Context

In the study successions, the climax of the fossiliferous preservation and of the organic carbon accumulation was matched with the starting of an important transgressive phase. The development of this same transgression successively brought important environmental modification. In the majority of the Lombardy Region, as in other Alpine areas, generalized deepening occurred. Carbonate platforms and reefs underwent severe ecological stress and were eventually drowned under the euphotic zone (Fig. 7). During this period, the basin was probably characterized by nutrient-rich waters, with reduced salinity, as suggested by the Iron-Sulphur-Organic systematics (Burchell, 1988; Stefani & Burchell, 1990). Temporary increase in the concentration of marine organic nutrients was probably produced by short lived interruption of sea-water stratification. Important influx of continental organic matter is also recorded in the coeval organic carbon rich rocks, suggesting an increased input of the continental nutrients.

Precise correlation between basinal and platform successions is often difficult, but it is clear that many carbonate platform areas experienced some deepening, with the area reduction of emerging islands and stromatolitic tidal flats, and the spread of subtidal lagoons, rich in large pelecypods faunae (megalodonts and conchodonts). Poorly oxygenated environments, lacking bioturbation, developed also in shallow intraplatform settings (Burchell & Stefani, 1992). The carbonate platform at that time generally lacked true buildup margins, whereas storm dominated oolitic and bioclastic shoals developed. After transgression, during the shallowing evolution of the Lombardy Region, storm dominated muddy ramps (Read, 1985) progressively developed, connecting the basin with the survived carbonate platforms. These ramp settings were characterized by mixed terrigenous-carbonate sedimentation. The environmental oxygenation probably decreased moving downwards along the slope. These areas were colonized by poorly diversified mollusc faunae, often very rich in individuals. Similar monotonous faunae, dominated by filter-feeder pelecypods (nuculas, rhaetaviculas) and sediment-feeder crustacean coprolites, characterized also the low energy environments that there developed on the drowned intrabasinal palaeohighs. The flat top of many of the previous carbonate highs however lacked any sedimentation, and only thin hard-grounds were therefore formed. The slope of the former carbonate highs were progressively overlapped by argillaceous muds (drowning unconformity, Schlager, 1989), but important gravitational instability survived, testified by argillaceous debris-flow deposits and widespread slumping, affecting also important fossiliferous levels (e.g. Ponte Giurino). The depression bottom was characterized by disoxic conditions. Therefore the basinal portion of the argillaceous succession generally lacks indigenous faunae.

### The faunae

The faunae are preserved in discrete unbioturbated levels within the lower transgressive portion of the argillaceous successions (Lower Mb. of the Argillite di Riva di Solto). The organisms were preserved within the

poorly oxygenated depressions inherited from the former wholly carbonate palaeogeography. The main fossiliferous localities are up to now known in central Lombardy (Bergamo Province, especially at Ponte Giurino). These fossiliferous levels are dominated by small pholidophorid fishes and by crustaceans (decapods and thylacocephalans) which constitute the most abundant fraction of the fauna. The argillaceous levels have revealed a few well preserved soft-bodied organisms such as rare annelid worms (eunicid, unpublished data, and aphroditid errant polychaetes, Alessandrello & Teruzzi, 1986) and jellyfishes. Rare well preserved terrestrial insects have also been found (Whalley, 1986).

Crustaceans are quite abundant. Decapod fauna shares just a few species with the lowstand associations; moreover, decapods are here more abundant and diversified.

Just a few genus (*Palaeodusa*, *Glaessnericaris*, and *Archaeopalinurus*) are present with the same species in both the stratigraphic levels. Even these forms show great differences in frequency. The penaeid shrimp *Palaeodusa* is often abundant in the basinal carbonatic succession, but it is quite rare in the younger levels; on the contrary the astacid crustacean *Glaessnericaris* is rare in the older fossiliferous levels, but it is abundant in the argillaceous units. Only the small spiny lobster *Archaeopalinurus* is comparatively common in both stratigraphic levels. The two decapod faunae show great ecological differences. Whereas natant forms dominated the older decapod faunae, here the benthic forms prevail. For instance in the main fossil locality (Ponte Giurino) benthic species (astacids and palinurids) represent about three quarters of the decapod fauna; moreover the large majority of the natant species (penaeids and carideans) consists of probably benthic forms (Garassino & Teruzzi, 1992). Benthic thylacocephalan crustaceans are more numerically abundant but less diversified in the argillaceous levels than in the older units (in the Argillite di Riva di Solto the only genus *Atropicaris* is known, Arduini, 1988; Arduini & Brasca, 1984). Isopod crustaceans are rare also in this unit. No corals, brachiopods or echinoderms have been found in these younger associations.

These argillaceous deposits show an impoverished vertebrate fauna with respect to that of older phase. Fishes are mainly represented by small pholidophorids, whereas durophagous forms are rare (Tintori et al., 1985). Taxonomic diversity of the fish association is generally comparatively reduced. Reptiles are represented only by a recently discovered flying form.

## Palaeoecological interpretation

The important faunistic changes recorded by the superimposed fossiliferous levels occurred over a geologically short time span and clearly reflect ecological modifications related to transgression. This transgression was matched with the drowning of active encrusted reefs and with a strong reduction in the carbonate production. The reduced sea water salinity, the increased turbidity and the nutrient excess probably played an important role in the carbonate high demise. Wide areas moved into disphotic and aphotic conditions, whilst soft argillaceous sea bottom became common.

The deepening evolution and the death of the active wave resistant reefs explain the lack of terrestrial vertebrates, and the strong reduction of durophagous forms in these associations. Benthic crustaceans and filter feeder organisms were adapted to the poorly oxygenated, nutrient rich sea water that developed after transgression. Acromys: MSNM = Museo Storia Naturale Milano; MSNB = Museo Scienze Naturali Bergamo; MBSN = Museo Brebano Scienze Naturali.

Acknowledgements - We would like to thank Dr. Anna Paganoni, Curator of the Museo Civico di Scienze Naturali of Bergamo for her kind collaboration. Part of the field work was supported by research grant of the C.N.R. (Grant n. 8900343054, A. Bosellini).



Fig. 8 — *Atropicaris rostrata*, holotype, Ponte Giurino (BG) (x 3,5), MSNM i 6070.

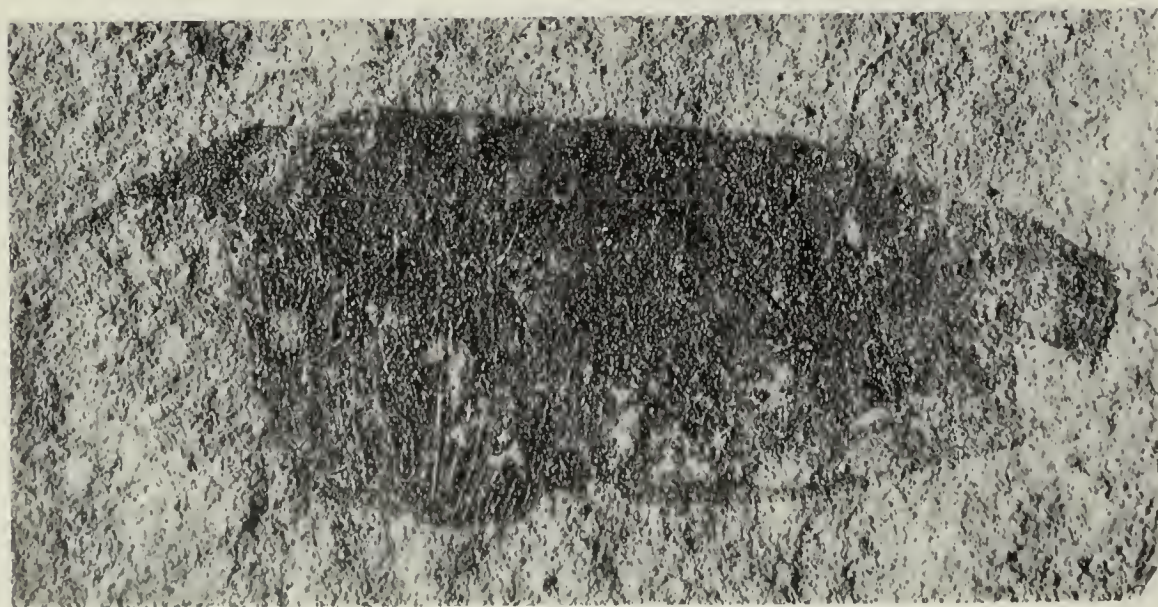


Fig. 9 — *Microcaris minuta*, holotype, Cenc (BG) (x 9), MSNB 3140.



Fig. 10 — *Archaeopalinarus levis*, Ponte Giurino (BG) (x 1), MSNM i 10747.

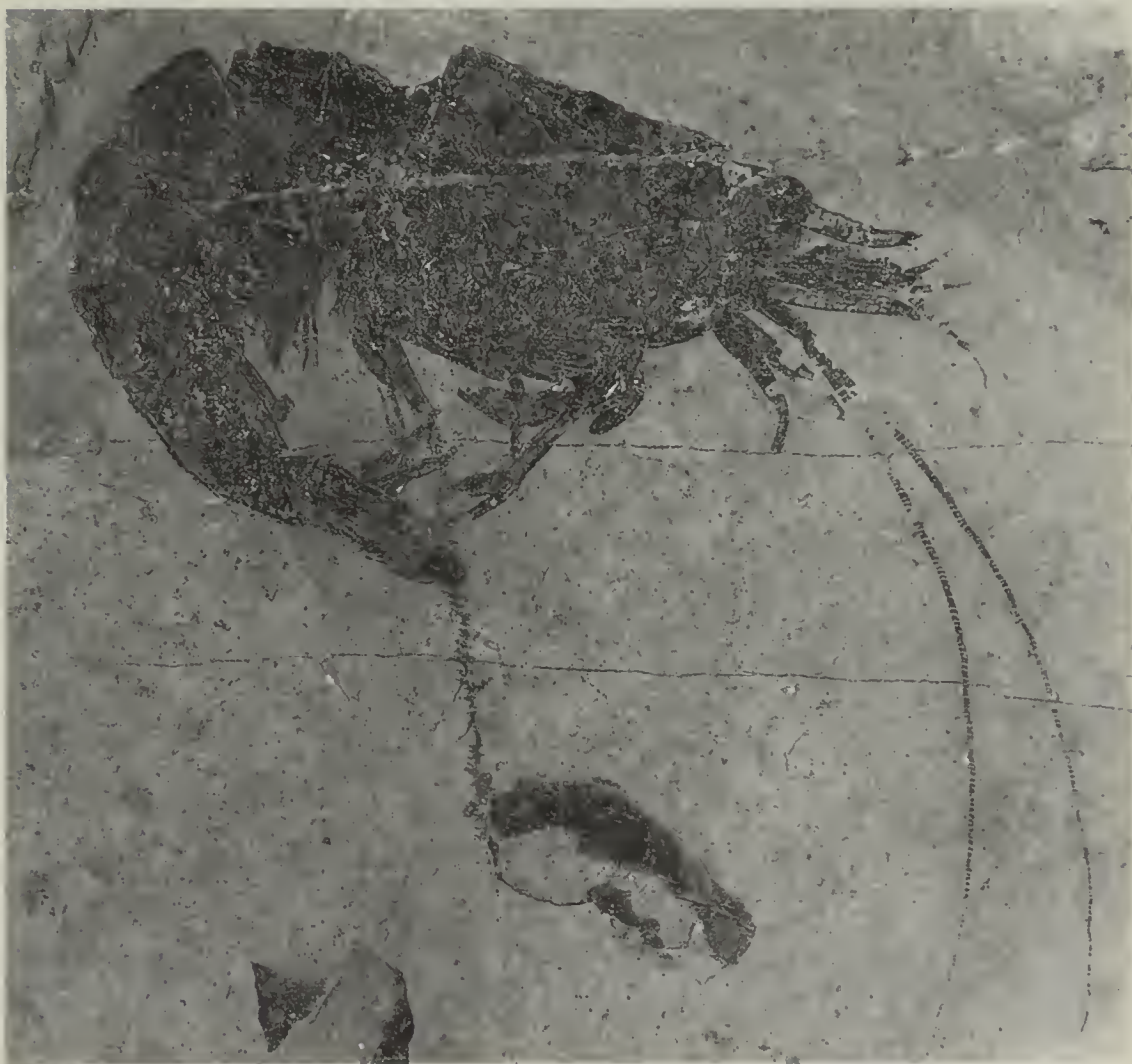


Fig. 11 — *Antrimpos noricus*, Cene (BG) (x 3), MSNB 3381.



Fig. 12 — *Pseudocoleia mazzolenii*, holotype, Ponte Giurino (BG) (x 4,5), MSNM i 12467.

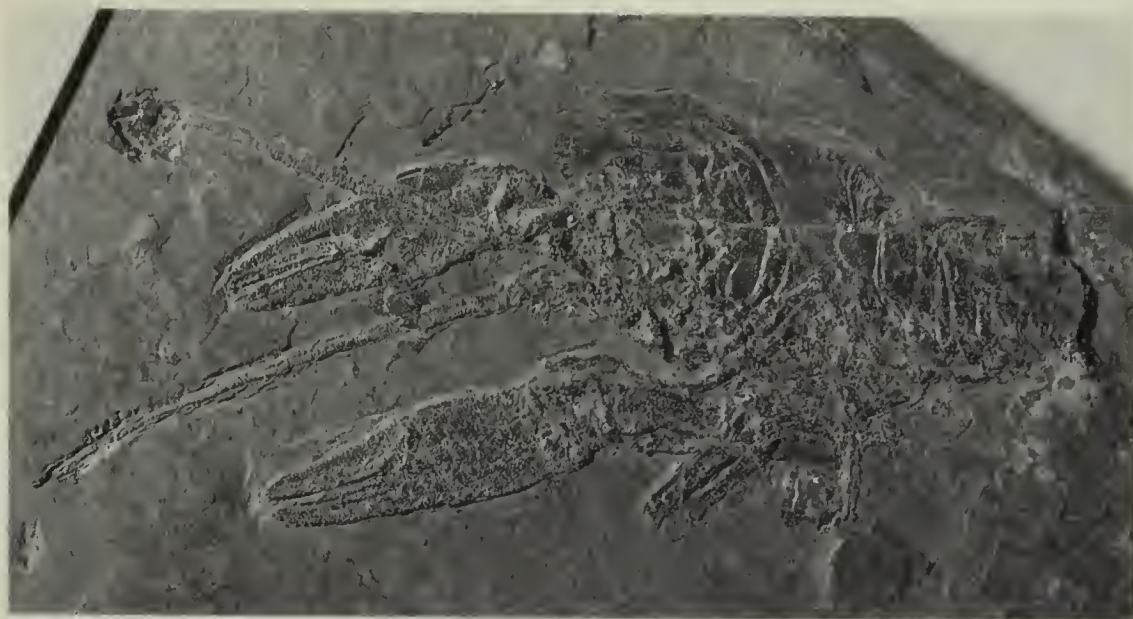


Fig. 13 — *Glaessnericaris macrochela*, holotype, Ponte Giurino (BG) (x 1,2), MSNB 4202.



Fig. 14 — *Psephoderma alpinum*, Endenna (BG) (x 0,2) MSNM V 527.

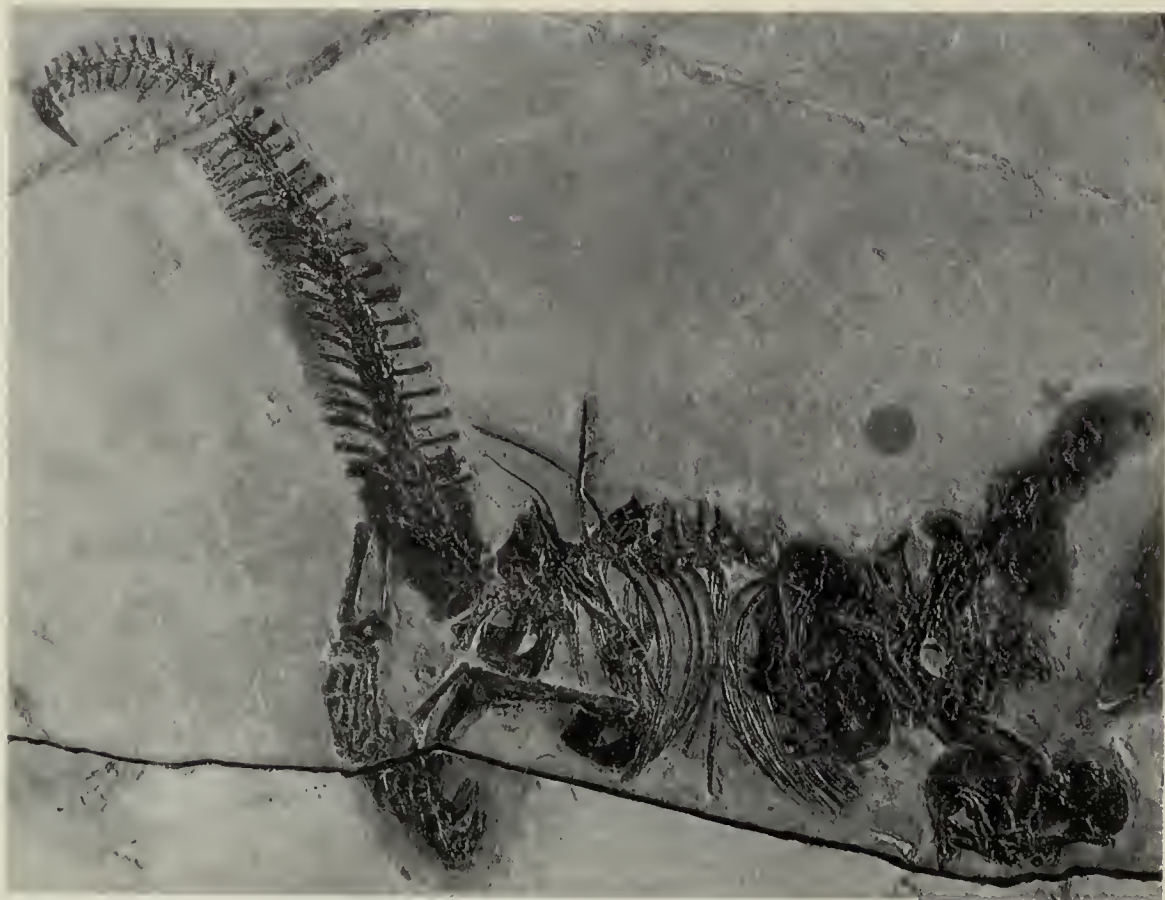


Fig. 15 — *Drepanosaurus unguicaudatus*, holotype, Endenna (BG) (x 0,3), MSNB 5728.

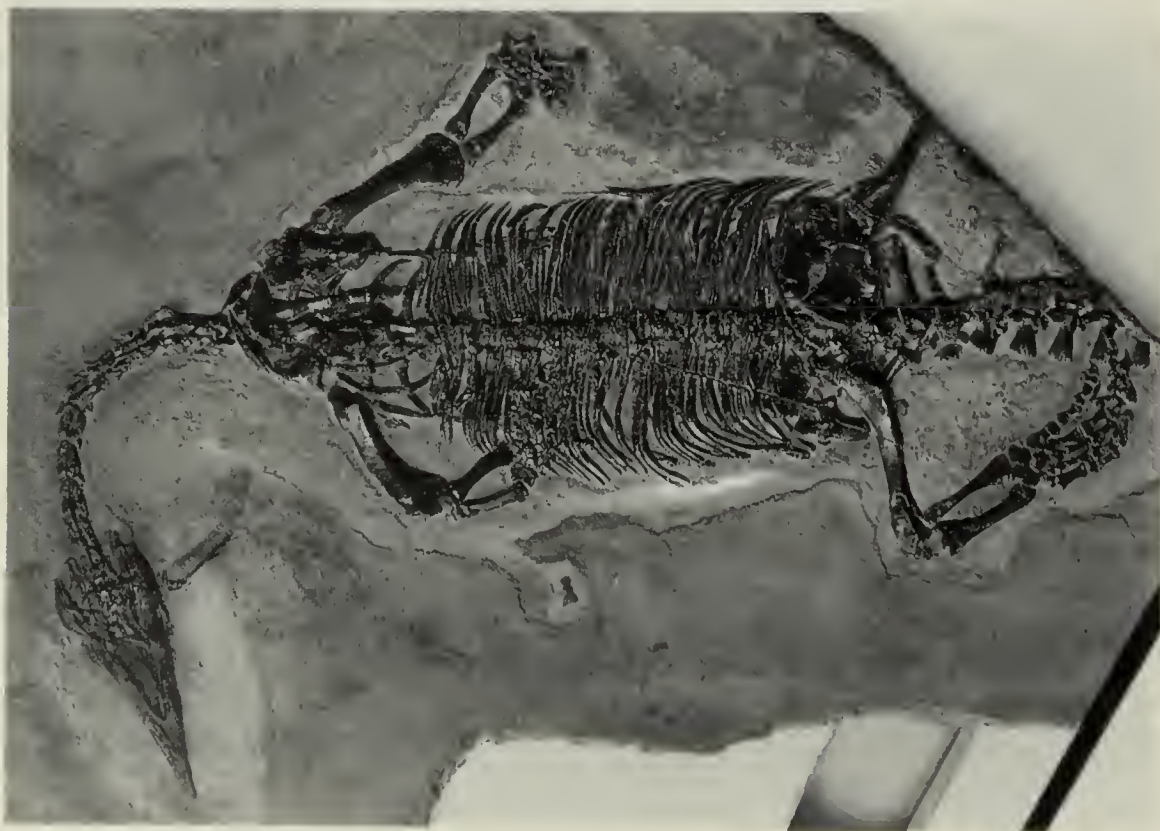


Fig. 16 — *Endennasaurus acutirostris*, holotype, Endenna (BG) (x 0,3), MSNB 5170.

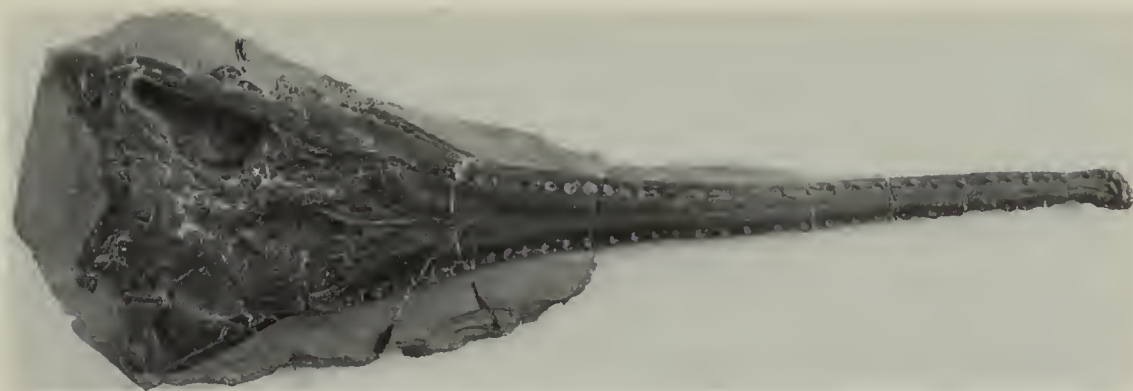


Fig. 17 — *Mystriosuchus* cfr. *planirostris*, Endenna (BG) (x 0,2), MBSN 2.



Fig. 18 — *Aëtosaurus* *ferratus*, Cene (BG) (x 2), MSNB 4864.

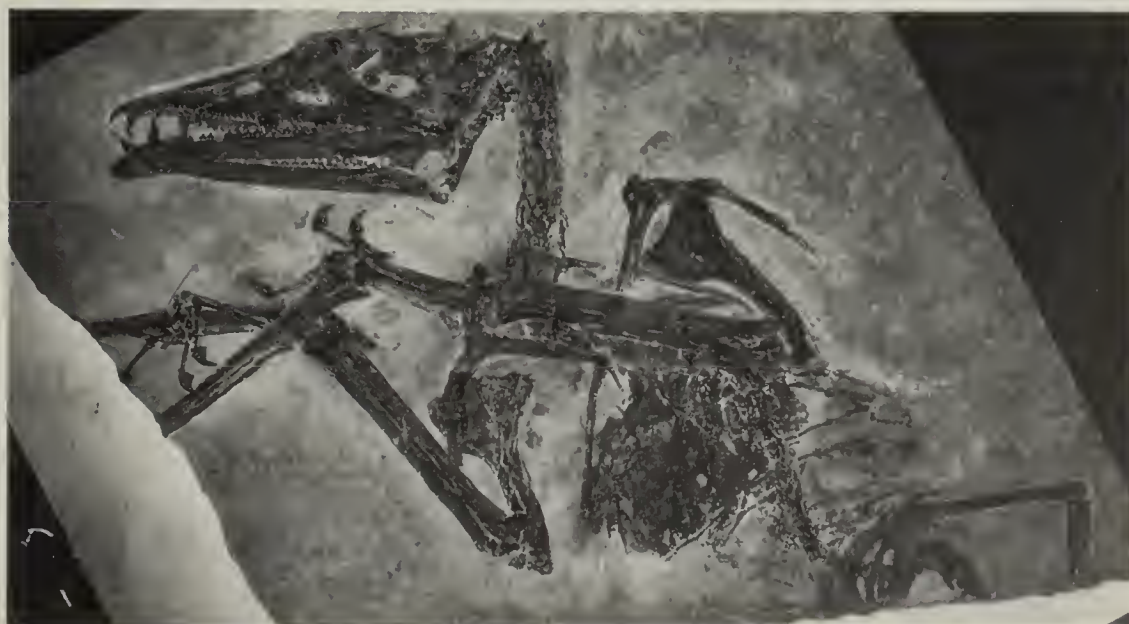


Fig. 19 — *Eudimorphodon* *ranzii*, holotype, Cene (BG) (x 0,5), MSNB 4864.

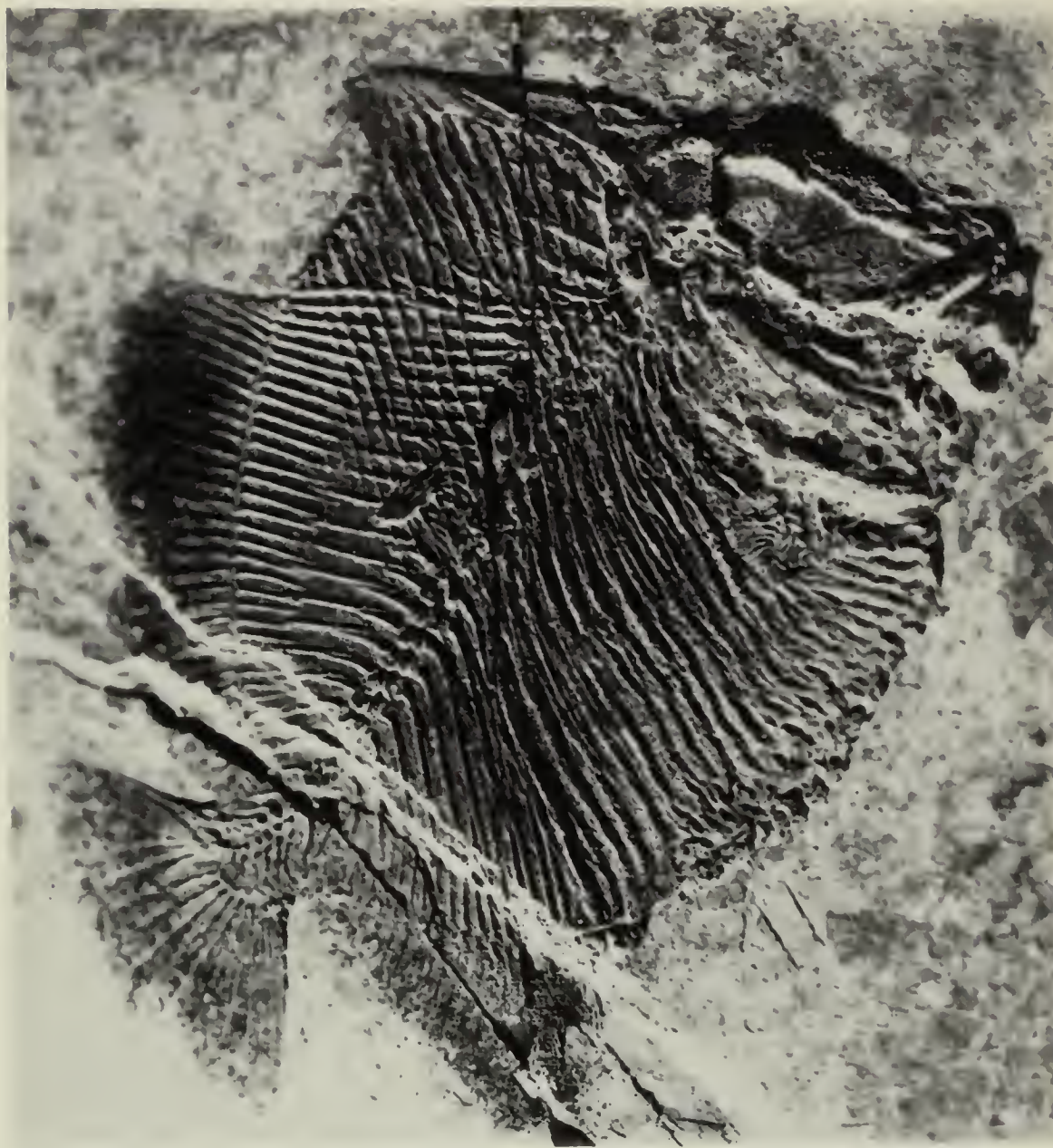


Fig. 20 — *Brembodus ridens*, holotype, Endenna (BG) (x 1), MSNB 4898.

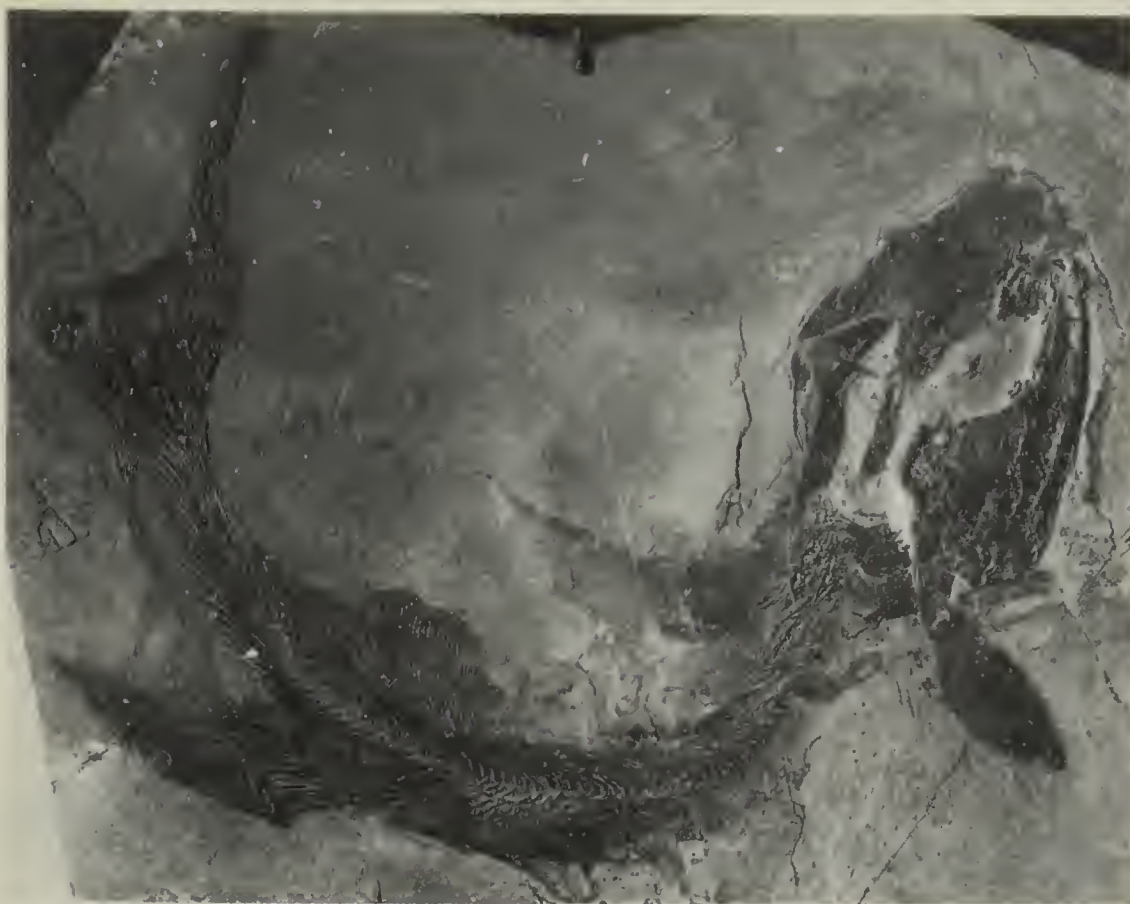


Fig. 21 — *Birgeria acuminata*, Cene (BG) (x 0,3), MSNB 4850.

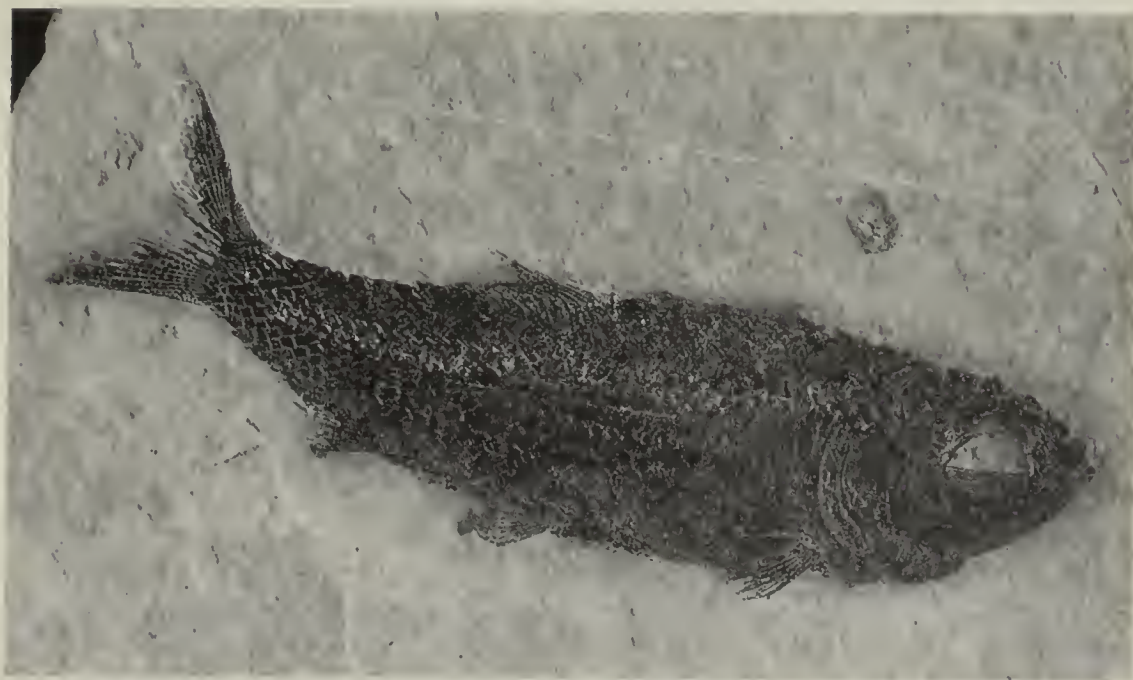


Fig. 22 — *Pholidorhynodon malzanii*, Cene (BG) (x 1,5), MSNB 3849.

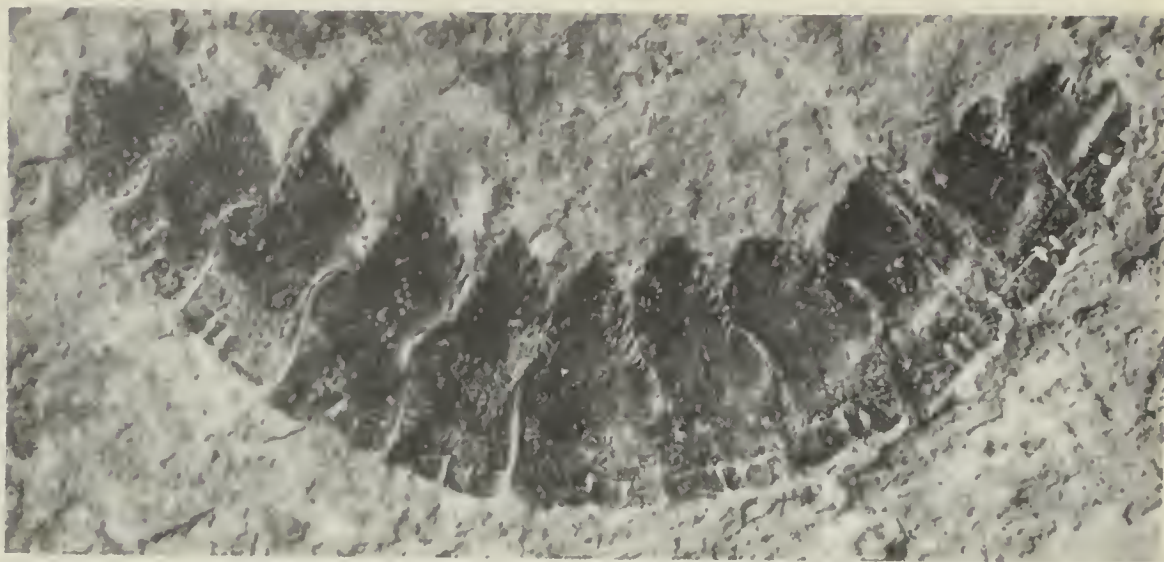


Fig. 23 — *Pseudodalatias barnstonensis*, Cene (BG) (x 7), MSNB 4557.

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